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SHORTER ARTICLES AND DISCUSSION

VARIATION, CORRELATION AND INHERITANCE OF FERTILITY IN THE MAMMALS

THE purpose of this review is to give an outline of the problems of fertility in the mammals (exclusive of man) which may be solved by the application of biometric formulæ to statistical data, to furnish an index to the available statistics, and to indicate the results to which the statistical analyses of the raw observations have led. Many of the biometric constants are published here for the first time.

TYPE AND VARIATION IN FERTILITY

The most fundamental biological questions which can be asked concerning series of data on fertility *considered quite independently of any other characteristic of the organism, its ancestry or its environment* are three:

(*a*) What is the typical and average fertility of different species or races?

(*b*) What is the variation, within the race, in reproductive activity as compared with that of variation in the degree of development of somatic characters?

(*c*) May fertility, like the bodily attributes of organisms, be described by mathematical curves?

With more comprehensive data concerning other characteristics of the individual organism, its ancestry or environment, more varied problems may be investigated, but none of more fundamental importance.

With respect to (*a*) it need only be said initially that biologically a knowledge of the number of offspring characteristic of a species has the same importance as a knowledge of any other of its peculiarities. That species may differ widely in fertility as in other characteristics is obvious without the collection of extensive statistics or the application of mathematical formulæ. It is only in a consideration of relatively *slight* differences in fertility in *nearly related* species or races or in individuals of the same race existing under various conditions, that biometric work became indispensable. It is just here, too, that the purely descriptive significance of fertility gives way to genetic, economic and sociological sources of interest.

As yet information on these subjects is all too meager. Lloyd[1] has emphasized slight differences in fertility in species formation in the rodents. Donaldson[2] has brought together the available data for fertility in the rat. For swine, Rommel[3] and Bitting[4] have given extensive data for different breeds and periods. Further records are available for swine from the studies of Wentworth and Aubel to be discussed below. Equations for theoretical curves of distribution of number of young per litter in Rommel's series have been worked out by Surface.[5] Large masses of statistics have been extracted from the herd books for sheep by Rietz and Roberts. Taken altogether, only a beginning has been made in a field that has not merely great biological interest, but in certain of its bearings is of material economic importance.

The most extensive and exact work on differences in fertility has been done on man, but a discussion of this subject falls outside the scope of the present review.

Since data for the solution of the problems of group (*a*) are as yet inadequate, it is idle to attempt any detailed discussion of those of group (*b*) and (*c*). Data for such purposes are, however, now becoming available much more rapidly than heretofore.

BIRTH ORDER AND LITTER SIZE

Fairly large series of records showing the relationship between birth order and litter size are now accessible.

Minot[6] has given data for the relationship in guinea pigs. The averages which may be computed from these are:

Order of Litter	F	Mean Size
First	51	1.96
Second	29	2.97
Third	15	2.80
Fourth	4	3.50

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[1] Lloyd, R. E., "The Inheritance of Fertility," *Biometrika*, **8**: 244–247, 1911.

[2] Donaldson, H. H., "The Rat," pp. 22–23, 1915.

[3] Rommel, G. M., "The Fecundity of Poland China and Durac Jersey Sows," Circ. U. S. Dep. Agr., Bu. Anim. Ind., 95, 1906.

[4] Bitting, A. W., "The Fecundity of Swine," Ann. Rep. Ind. Agr. Exp. Sta., **10**: 42–46, 1897.

[5] Surface, F. M., "Fecundity of Swine," *Biometrika*, **6**: 433–436, 1906.

[6] Minot, C. S., "Senescence and Rejuvenation," *Jour. Phys.*, **12**: 97–153, 1891.

Crampe[7] many years ago showed from his extensive data on rats that the maximum fertility was on the second litter. King and Stotsenberg[8] have recently given data which lead to the following averages:

Order of Litter	*F*	Mean Size
First	21	6.24
Second	21	7.71
Third	18	7.06
Fourth	15	6.40

Pearson and Weldon have shown[9] that in mice there is an increase in the mean number of young from the first to the third litter, thus:

Order of Litter	Mean Offspring
First	5.46
Second	5.57
Third	5.76

For the rabbit Bailey, *fide* Hammond,[10] gives the values:

Order of Litter	Mean Offspring
First	5.58 ± 0.32
Second	7.25 ± 0.41
Third	7.08 ± 0.38

Such data as these are of obvious importance in the physiology of reproduction in the mammals. They will be of far greater value when it is possible to determine the influence of the actual age of the mother as well as of the order of birth upon fertility. Detailed records of size as well as of number of offspring and of mortality would also be of great importance.

RELATIONSHIP BETWEEN FERTILITY AND SOMATIC CHARACTERS

The interrelationship between fertility and somatic characters is a subject which may have a morphogenetic, genetic or economic interest.

Reference to some of the earlier literature has already been made[11] in a memoir dealing with plant materials and certain special problems more minutely analyzed on further sets of data.[12]

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[7] Crampe, H., "Zucht-Versuche mit zahmen Wanderratten. I. Resultate der Zucht in Verwandschaft," *Landwirths. Jahrb.*, **12**: 389–449, 1883.

[8] King, H. D. and J. M. Stotsenberg, "On the Normal Sex Ratio and the Size of the Litters in the Albino Rat (*Mus norvegicus albinus*)," *Anat. Record*, 9: 403–420, 1915.

[9] *Biometrika*, 7: 384, 1910.

[10] Hammond, J., "On Some Factors Influencing Fertility in Domestic Animals," *Jour. Agr. Sci.*, 6: 263–277, 1914.

In the mammal, the relationship between fertility and somatic characters may be determined from (*a*) the somatic characters of an individual mother and her fertility, or (*b*) the characteristics of the progeny which serves as the measure of the fertility of a mother. Obviously, these two methods of operation are biologically not at all comparable.

The economic importance of the possible correlation between bodily characteristics and fertility has naturally given rise to many popular beliefs concerning the existence of such a relationship. Wentworth and Aubel[13] have, however, found no evidence of such in a comparison of the mean litter size in ''large type'' and ''small type'' hogs.

Pearson has shown[14] from Captain Lloyd's data[15] that there is a sensible and almost linear relationship between weight of mother and number of young in litter in Poona and Belgaum rats. The intensity of the correlation is, however, low, of the order $r = .160$.

Data for the full interpretation of such relationships are much needed but not as yet available. The problem is evidently one of great complexity. As Pearson points out, at certain stages of pregnancy the number of young might actually influence, by its own contribution, maternal body weight.[16] Furthermore, in these rodents growth continues notwithstanding pregnancy, and one might expect some correlation between weight of mother and size of litter as a resultant of the relationship between the age of the mother and her own weight and the age of the mother and the size of her litter.

Minot found that the over-gain in weight of pregnant guinea pigs is not all lost after delivery[17] and Watson[18] many years ago adduced evidences to show that females which have borne young are heavier than unmated controls. Whether the effect of bearing young is cumulative in such a way as to influence the correlations in Captain Lloyd's series is not yet evident.

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[11] Harris, J. Arthur, *Biometrika*, 8: 52–65, 1910.

[12] Harris, J. Arthur, *Amer. Jour. Bot.*, 1: 398–411, 1914.

[13] Wentworth, E. N. and C. E. Aubel, *Jour. Agr. Res.*, 5: 1148, 1916.

[14] Pearson, K., ''Darwinism, Biometry and Some Recent Biology,'' I, *Biometrika*, 7: 368–385, 1910.

[15] Lloyd, R. E., ''The Relation between Fertility and Normality in Rats,'' *Rec. Ind. Mus.*, 3: 261–265.

[16] Minot (*Journ. Phys.*, 12: 141–145, 1891) has shown that in the guinea pig there is a relatively enormous over-gain in weight before delivery.

[17] Crampe (*loc. cit.*) has given certain data on the weight of mothers after the first and second deliveries in the rat.

[18] Watson, J. B., ''The Effect of the Bearing of Young upon the Body

Taking these various factors into account, there seems little ground for believing that there is any material correlation between the fertility of a mammalian female and her measurable somatic characters.

There is an obvious physiological and morphogenetic interest attaching to the correlations between the number of individuals born in a litter and the characteristics of these individuals.

Consider first the correlations between number of pigs in the litter and number of nipples, in swine. For Parker's[19] and Bullard's data the values are:

For males, $r = .0810 \pm .0121$,
For females, $r = .0324 \pm .0124$.[20]

These are numerically low, but both are positive, and may possibly be significant in comparison with their probable errors. They may indicate morphogenetic relationships between the vigor of the mother as indicated by the number of her young and the characteristics of these young.

These positive correlations for number per litter and number of nipples are of interest in connection with the *negative* correlation for number in the litter and mean weight of individuals suggested many years ago by Minot,[21] who states that in guinea pigs the size of the animals at birth depends to a considerable degree upon the number of young in a litter: the larger the litter the smaller the animals at birth. Fortunately Minot has given data from which approximate[22] values of the correlation between number of individuals per litter and birth weight may be compared. The results are:

Weight and the Weight of the Central Nervous System of the Female White Rat,'' *Jour. Comp. Neur. Psychol.*, 15: 514–524, 1905.

[19] Parker, G. H. and C. Bullard, ''On the Size of Litters and the Number of Nipples in Swine,'' *Proc. Amer. Acad. Arts and Sci.*, 49: 399–426, 1913.

[20] Parker and Bullard give the correlation $r = .0035 \pm .0124$ for females only. This is evidently erroneous. Both values given here have been calculated from their data.

[21] Minot, C. S., ''Senescence and Rejuvenation. I. On the Weight of Guinea Pigs,'' *Jour. Phys.*, 12: 96–153, 1891.

[22] The only difficulty lies in the fact that his Tables VII and VIII do not contain the same number of individuals.

$$\begin{aligned}&\text{For males,} && r_{nw} = -.437 \pm .039,\\ &\text{For females,} && r_{nw} = -.431 \pm .044,\\ &\text{For all,} && r_{nw} = -.430 \pm .029.\end{aligned}$$

The results for males and females are in remarkable agreement. Evidently there is a large influence of the number born upon the weight of the individual.[23]

If the results be expressed in terms of regression of weight of individual upon number in litter the equations are:

$$\begin{aligned}&\text{For males,} && w = 87.626 - 5.214\,n,\\ &\text{For females,} && w = 84.375 - 4.741\,n,\\ &\text{For all,} && w = 86.006 - 4.960\,n.\end{aligned}$$

King[24] has given direct evidence for the influence of weight of mother in the weight of the young at birth.

> Very young females and those that have passed their prime have smaller litters, as a rule, than females at the height of their reproductive powers.

And again,

> The body weight of a female influences the birth weight of her young chiefly because it depends on the two more important factors of age and physical condition.

Finally it may be noted that in the case of sheep the size at birth and rate of development of twin and triplet as compared with the single lambs is a problem of very real economic importance. Both Bell and Marshall have considered this phase of the question. Unfortunately no extensive quantitative data are available for analysis on this point.

INHERITANCE OF FERTILITY

Biologically all recent studies on the inheritance of fertility differ from the classic memoir of Pearson, Lee and Branley-

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[23] That factors other than number per litter may profoundly influence birth weight may be seen at once by determining the correlation between the weight of the individual pigs born in litters of two as given in Minot's Table XI. Using symmetrical tables I find for the correlation between the weight of the two individuals

$$r_{w_1 w_2} = .686 \pm .046.$$

This similarity in weight is probably due in part to hereditary and in part to environmental factors.

[24] King, H. D., "On the Weight of the Albino Rat at Birth and the Factors that Influence It," *Anat. Rec.*, 9: 213–231, 1915.

Moore[25] on fertility in man and fecundity in race horses in that they deal with the number of young produced at a single birth instead of with the total young produced during the reproductive period or the ratio of the number of young actually born to the number which might have been produced under the circumstances.

For Poland China sows Rommel[26] and Rommel and Phillips[27] found values of the correlation between the size of litters in which dam was farrowed and size of litters produced by daughters ranging from .1088 to .0032, the values decreasing with moderate regularity as the daughters became older. For all ages they find the correlation $r = .0601$, and conclude that fertility is slightly but definitely inherited.

George (*fide* Wentworth and Aubel, *loc. cit.*) worked out four supplementary series in Poland China swine with the results:

Daughter and dam, $r = .0615 \pm .0390$,
Dam and grandam, $r = .1147 \pm .0343$,
Daughter and maternal grandam, $r = .0025 \pm .0392$,
Daughter and paternal grandam, $r = .0508 \pm .0392$.

All of these values are positive, but they are very small and no one of them may be considered statistically trustworthy in comparison with its probable error.

Weldon and Pearson[28] give a series of six relationships, both parental and grandparental, for size of litter in mice, with the result that no correlation whatever could be demonstrated.

Wentworth and Aubel[29] have considered the possibility of the segregation of litter size in the two first descendant generations of matings between boars and sows farrowed in litters of various sizes by determining the standard deviation of the number per litter in the so-called F_1 and F_2 generations. Let l be the number of pigs in the litter in which an individual was farrowed, d the number of pigs in the litter in which its dam was farrowed, and S and D the numbers in the litters in which the grandsire and grandam were farrowed. Then, the authors reason, if fertility be due to factors which differ in the grandsire, S, and the grandam, D, and if Mendelian segregation occurs in the fashion assumed by several of these who have worked on quantitative characters, one should expect the mean value of the standard deviation of litter size in cases in which D and S differ widely to be higher than the mean value in cases in which they are closely similar. There is no conclusive evidence of such greater segregation in the F_2 from dissimilar grandparents.

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[25] Pearson, K., A. Lee and L. Branley-Moore, *Phil. Trans. Roy. Soc. Lond., A,* 192: 257–330, 1899.

[26] Rommel, G. M., "Inheritance in the Female Line of Size of Litters in Poland China Sows," *Biometrika,* 5: 203–205, 1906.

[27] Rommel, G. M., and E. F. Phillips, "Inheritance in the Female Line of Size of Litter in Poland China Sows," *Proc. Amer. Phil. Soc.,* 45: 245–264, 1906.

[28] Pearson, K., "On Heredity in Mice from the Records of the Late W. F. R. Weldon. I. On the Inheritance of the Sex Ratio and of the Size of Litter," *Biometrika,* 5: 436–449, 1907.

[29] Wentworth, E. N., and C. R. Aubel, "Inheritance of Fertility in Swine," *Jour. Agr. Res.,* 5: 1145–1160, 1916.

Now the data published by Wentworth and Aubel permit the consideration of several additional questions of considerable interest in connection with the problem of the inheritance of fertility. Thus from the mean litter sizes in their Table II and the distributions of litter size in the three generations in their Table IV, it is quite possible to calculate *approximately*[30] correct correlations for the relationship between size of litter in different generations. Thus the formula:

$$r_{xy} = \frac{\Sigma(xn\bar{y}_x) - [\Sigma(x)/N][\Sigma(n\bar{y}_x)/N]}{\sigma_x \sigma_y},$$

where the bars denote the means of the y (descendant) litters associated with particular, x, classes of ascendant litters, leads to the values:[31]

$$r_S = .071 \pm .023, \quad r_{Dd} = .126 \pm .022,$$

$$r_{Sl} = .120 \pm .022, \quad r_{Dl} = .100 \pm .022.$$

Superficially considered, these values seem in excellent agreement with those published by Rommel and others, but the fact that r_{Sd} has a value which is possibly significant statistically, should at once arouse suspicion, for surely there is no genetic reason (excepting possibly non-viability of sperm or the production of duplicate twins through an influence of the sperm upon the egg) why there should be a correlation between the size of the litter in which a boar was farrowed and the size of litter in which his daughter was farrowed. Mistrust is heightened by the fact that r_{Sd} is actually though perhaps not significantly lower than r_{Sl}, whereas on the female side $r_{Dd}r > r_{Dl}$. Obviously there is no genetic reason for a correlation between the size of the litters in which the grandsires, *S*, and the grandams, *D*, were farrowed. But columns 1–3 of Table II of Wentworth and Aubel actually give:

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[30] Unfortunately there are inconsistencies in these tables which show the existence of typographical errors precluding exact constants.

[31] Unfortunately data for the determination of r_{di} are wanting.

$$r_{SD} = .121 \pm .022,$$

a value quite as large as those recorded above.

Such a correlation might arise (*a*) through the existences in the pens of different breeders of strains slightly differentiated with respect to fertility, (*b*) through differences in the conditions in which different breeders maintained their pens, providing such conditions affect litter size, or (*c*) through actual dishonesty of certain breeders in reporting the size of litters for herd-book publication.

Such differentiation, if it exists, would also account in part at least for the correlations hitherto regarded as due to inheritance. The whole problem is evidently one of great complexity and requiring far more detailed investigation than it has yet received.

The problem of the inheritance of the production of twins in sheep which has been studied experimentally by Alexander Graham Bell for the past several years, has recently been investigated statistically by Rietz and Roberts.[32]

There seems to be unmistakable evidence of inheritance, or at least of ascendant influence,[33] upon descendant characteristics. This may be most clearly seen by comparing the average number per litter resulting from certain matings.

Thus for the parental relationship the results are:

When sire and dams are singles	1.3452 ± 0.0059
When sire is single and dam is twin	1.4171 ± 0.0067
When sire is twin and dam is single	1.3946 ± 0.0073
When sire is twin and dam is twin	1.4548 ± 0.0088
When either sire or dam is a triplet	1.6076 ± 0.0300
Mean of all offspring	1.3979 ± 0.0035

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[32] Rietz, H. L. and E. Roberts, "Degree of Resemblance of Parents and Offspring with Reference to Birth as Twins for Registered Shropshire Sheep," *Jour. Agr. Res.*, 4: 479–510, 1915.

[33] In the case of slight relationships between parents or earlier ancestors and offspring there is always danger of attributing to heredity the influence of purely physiological factors.

Or for the dams and grandams:

When dams and grandams are singles	1.3446 ± 0.0057
When the dams are singles and grandams twins	1.3689 ± 0.0070
When the dams are twins and grandams are singles	1.4245 ± 0.0071
When the dams are twins and grandams are twins	1.4559 ± 0.0078
When either dam or grandam is a triplet	1.545 ± 0.037

Finally for the maternal grandams alone:

When the maternal grandams are singles	1.3784 ± 0.0045
When the maternal grandams are twins	1.4120 ± 0.0052
When the maternal grandams are triplets	1.556 ± 0.033

It is quite out of the question to review in any detail the thorough analysis of the numerous interrelationships deduced from the many thousands of records abstracted by the authors from the Shropshire record. Their data seem to be free from the possible objection raised against the swine records above, for the correlation between sire and dam, which may be deduced from their Table I, is only $r = .0058 \pm .0070$.

The intensity of correlation between the size of litter in which an individual is born and the size of the litter in which his sire or dam or grandsire or grandam was born is very low. The maximum relationships are in fact of the order $r = .08$.

In the parental relationships the correlation between the size of litter in which the sire was born and the size of the litter in which his offspring were born seems to be significant, as well as that between the size of the litter in which the dam was born and the number of the offspring. The mean number of offspring are:

When the sire was born single	1.3787 ± 0.0045
When the sire was a twin	1.4220 ± 0.0057
When the sire was a triplet	1.683 ± 0.045

Note the agreement of this result with that obtained by Wentworth and Aubel. An explanation on the basis of identical twins induced by the characteristics of the sperm, or of partial impotency in certain males, should be sought by those who have experimental facilities.

There seems to be a significant correlation between maternal grandams and offspring, but it is impossible to assert any trustworthy correlation for the other grandparents.

INFLUENCE OF ENVIRONMENT ON FERTILITY

Marshall[34] while emphasizing the importance of the hereditary factor in multiple births in sheep, adduces evidences for the great importance of feeding as a factor in the production of twins and triplets. His figures certainly show great and consistent differences in the produce of flocks which have received different treatment at and preceding tupping time. Unfortunately differences in breed may, but do not necessarily, cast some doubt on the interpretation of the data. The problem which he has attempted to solve by the analysis of schedules received from flock masters certainly deserves experimental study. Such investigations have actually been begun by Evvard who in a first[35] and second[36] and third[37] report on experiments with swine has given the results of various feeding upon the vitality of the offspring. Discussion of the data as they are presented in these papers falls outside the scope of a biometric review. Such work is, however, of great importance at a period of science in which heredity as contrasted with environment is apt to be assumed to be an all-important factor. It is a pity that such experiments as these of Marshall and Evvard can not be carried out in close cooperation with experts on the physiology of nutrition, so that differences in rations might be arranged on a uniform scale.

J. ARTHUR HARRIS

ON A BARNACLE, CONCHODERMA VIRGATUM, ATTACHED TO A FISH, DIODON HYSTRIX[1]

A SPECIMEN of the "sea porcupine," *Diodon hystrix* Linn., seen swimming near the surface and secured with a dipnet, was

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[34] Marshall, F. H. A., "Fertility in Scottish Sheep," *Trans. High. Agr.* Soc. Scotland, V, 20: 139–151, 1908.

[35] Evvard, J. M., "Nutrition as a Factor in Fetal Development," *Proc. Amer. Breed. Ass.*, 8: 549–560, 1912.

[36] Evvard, J. M., "Some Factors affecting Fetal Development," *Proc. Iowa Acad. Sci.*, 20: 325–330, 1913.

[37] Evvard, J. M., A. W. Dox and S. C. Guernsey, "The Effect of Calcium and Protein Fed Pregnant Swine upon the Size, Vigor, Bone, Coat and Condition of the Offspring," *Proc. Iowa Acad. Sci.*, 21: 269–278, pl. 31–35, 1914.

[1] Contributions from the Bermuda Biological Station for Research, No. 50.